Seasonal variation of photosynthetic properties of
Ecklonia cava (Laminariales, Phaeophyta)
in Nabet Bay, central Japan

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Abstract: The research was carried out to quantify the photosynthetic rates of a perennial seaweek Ecklonia cava Kjellman (Laminariales, Phaeophyta) with monthly samplings from April 1986 to April 1987. Photosynthesis and respiration were measured by a differential gas-volumeter in several bladelets. The photosynthesis-light curvves were different among bladelets almost every month; however, in winter, when all the bladelets were new, the curves were quite similar. On a frond area basis, the youngest bladelets showed higher net photosynthesis than the older ones, with highest Pmax values (44-49 \( \mu \)mol \( \text{O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1} \)) in early spring and lowest (19-31 \( \mu \)mol \( \text{O}_2 \cdot \text{cm}^{-2} \cdot \text{h}^{-1} \)) in autumn, the reproductive period. On a dry weight basis, the Pmax values showed a hierarchical order inversely related to the thickness of the bladelets, with a maximum in the 2nd bladelet and a minimum in the 11th. On a chlorophyll a basis, the hierarchical order was similar to that on a dry weight basis, but Pmax did not show any big seasonal variation. The respiration rate of each bladelet was quite stable throughout the year, except for the 2nd bladelet with two high peaks in November and February, the formation periods of autumn and winter bladelets respectively. The photosynthetic respose of E. cava blade is closely related to its growth process. The blade of this species apparently adjusts its pigment content to the prevailing light conditions in the surrounding water.

Introduction
As in terrestrial plants, light is the most important factor affecting the biology of seaweeds. Besides its primary importance in the photosynthesis, light is a signal for numerous photomorphogenetic responses such as reproduction, growth and distribution (Lüning, 1986, 1981; Novack, 1984; Lobban et al., 1985; Maegawa et al., 1987). The photosynthetic rates of large seaweeds have scarcely been studied due to the difficulties encountered in handling these algae (Drew, 1973; Jasby, 1978; Kremer, 1978; Littler and Littler, 1985). Yokohama and Ichimura, (1969) devised a differential gas-volumeter for measuring \( \text{O}_2 \) consumption or evolution by aquatic organisms, and several papers have been published dealing with the photosynthetic characteristics of various seaweeds (Yokohama, 1971, 1973a, b; Mizusawa et al., 1978; Oohusa, 1980; KayaTaya et al., 1985; Maegawa et al., 1987). This manometric method has been improved allowing easier measurements for macrophytes or small marine animals (Yokohama et al., 1986; Yokohama and Maegawa, 1988).

The sporophytes of Ecklonia cava Kjellman are widely distributed on rocky shores along the Pacific coast of central Japan. In previous papers (Aruga, 1981; Yokohama et al., 1987) it was reported that the standing crop of E. cava communities attains a maximum in summer and a minimum in winter; this is mainly related to the seasonal variation of the blade growth process (Haroun et al., 1989). Recently, Sakanishi et al. (1988) developed a suitable treatment of
tissue segments from the thalli of *Ecklonia* and *Eisenia* to measure the photosynthesis of these Laminariales species by the above-mentioned oxygen technique.

The present investigation was done to measure the photosynthetic rates of the pinnate blade of *Ecklonia cava* during one-year period. Another objective in the study was to investigate the relationship between physiological activity and the phenology of the blade. Finally, we try to relate the annual pattern of photosynthetic response to some possible environmental factors.

**Material and methods**

Morphologically, the *E. cava* sporophyte can be divided into three parts: a holdfast, a long stipe (more than 50 cm long in adult plants) and a pinnate blade composed of lateral bladelets (Hayashida, 1977; Margaawa and Kida, 1984). As in other species of Laminariales, primary growth is concentrated in the transitional zone between stipe and blade. When growth is initiated, the primary blade moves upward, developing several bladelets in both sides (usually with lateral protuberances); while the sporophyte erodes from the distal ends of both primary blade and bladelets.

The research was carried out at Shimoda Marine Research Center (S.M.R.C.), University of Tsukuba, close to Nabeta Bay, Shimoda (Izu Peninsula), with monthly samplings from April 1986 to April 1987. Every month 4 adult plants were randomly sampled from a homogeneous population of *E. cava* at 5 m depth (Fig. 1). All the plants were quickly transferred to S.M.R.C. and were kept in outdoor tanks supplied with flowing seawater before use. Special care was taken not to wound the frond and to protect them from direct sunlight. Pieces measuring 15 cm² were cut out from the central part of the 2nd, 5th, 8th and 11th bladelets longer than 10 cm as numbered starting from the proximal part of the blade. In January there were not 8th or 11th bladelets available due to the shortness of the blade. To avoid abnormal results caused by cutting, the pieces were kept in running seawater overnight in the laboratory (Sakanshi et al., 1988). At the same time, small discs (0.73 cm²) of the bladelets were taken and frozen for quantitative analyses of chlorophylls.

Photosynthesis and respiration were measured by a differential gas-volumeter adapted for large seaweed pieces, with four set of culture flasks of 250 ml capacity as the reaction and compensation vessels (Yokohama and Margaawa, 1985). All the measurements were done at 20°C and with an illuminance gradient of 0 to 20 klux (0-400 μE·m⁻²·s⁻¹) by using a slide projector with an incandescent lamp (Kondo, 100V 300W) as a light source. The illuminance was changed in a stepwise fashion with neutral density filters (Toshiba TND-50, -25 and -12.5). Illuminance and photon flux density were measured by a lux meter (Minolta T-1) and a quantum meter (LI-COR LI-185b/LI-192S).

The discs for the determination of chlorophyll content were ground with 90% acetone and the absorbances of the extract were measured at 630 and 664 nm with a dual beam spectrophotometer.
(Shimadzu UV-320). Chlorophyll a and c concentrations were calculated using the formulae of Jeffrey and Humphrey (1975).

All the procedures were repeated monthly at least with 3 replicates for each bladelet. Afterwards, a statistical analysis was applied and the average of all measurements for each bladelet was used as the monthly values for that bladelet.

As possible environmental control, the following parameters were studied: seawater temperature and Secchi disc depth as well as the length of daytime (Fig. 2). The seawater temperature at Nabeta Bay was daily obtained by the S.M.R.C. staff (Anon., 1981–1986). There is a minimum in mid-winter (February, 12.8 °C), and a maximum in late summer (August, 25 °C). As an indirect measure of light conditions in Nabeta Bay water, was used the Secchi disc depth measured in Sagami Bay off Shimoda (Hogetsu et al., 1977). The maximal values were found in mid-winter (20–24m) and the minimal ones were recorded during the summer months (13–18m). The same trend was also observed in Nabeta Bay. The seasonal variation of the length of daytime at Shimoda was obtained from the National Meteorological Datum.

Results

Photosynthesis-light curves

Photosyntheses-light curves are illustrated in Fig. 3 on a frond area bases, a dry weight basis and a chlorophyll a basis for the July, October, December and March samples. In all the cases, the photosynthetic rates increased with increase of illuminance within the range used in this study. The light-limited part of each curve was quite similar among the bladelets, but when the illuminance increased the response of each bladelet was different.

Seasonal variation of $P_{\text{max}}$

The net photosynthetic rates at 20 klux, henceforth considered as $P_{\text{max}}$, were maximal in winter-early spring (44–49 µmol cm$^{-2}$ h$^{-1}$, 5.3–9.2 µmol mg$^{-1}$ h$^{-1}$ and 1.3–2.2 µmol µg chlor a$^{-1}$ h$^{-1}$) and minimal in early autumn (19–30 µmol cm$^{-2}$ h$^{-1}$, 0.8–2.7 µmol mg$^{-1}$ h$^{-1}$ and 0.5–0.9 µmol µg chlor a$^{-1}$ h$^{-1}$). The $P_{\text{max}}$ on a dry weight basis began to increase as early as in November (in the 2nd bladelet), and reached maximal values in March, thereafter they gradually declined to the minimal values of September or October (Fig. 4). The decline of $P_{\text{max}}$ from winter to late summer was more drastic on a dry weight basis than on a frond area basis or on a chlorophyll a basis. The dominant hierarchical order of $P_{\text{max}}$ on a dry weight basis was 2nd, 5th, 8th and 11th bladelets from high to low performance; however, in mid-winter the $P_{\text{max}}$ values were quite similar among the bladelets. From November to January, the bladelets formed in autumn
Fig. 3. Photosynthesis-light curves of each bladelet and the average of *Ecklonia cava* blade on a frond area, on a dryweight and on a chlorophyll a bases in selected months (July, October and December 1986, and March 1987). □ 2nd, ▲ 5th, ○ 8th, △ 11th and ○ average.
showed specifically high photosynthetic rates.

Seasonal variation of respiration rates

Both on a frond area basis and on a chlorophyll \( a \) basis, the monthly average of respiration rate did not show any big variation, 2.7–4.8 \( \mu \text{mol} \cdot \text{cm}^{-2} \cdot \text{h}^{-1} \) and 0.1–0.2 \( \mu \text{mol} \cdot \text{mg}^{-1} \cdot \text{h}^{-1} \), during the period of study with relatively low values in December and March. On the other hand, the variations were bigger on a dry weight basis, 0.2–0.8 \( \mu \text{mol} \cdot \text{mg}^{-1} \cdot \text{h}^{-1} \) (Fig. 5).

Comparing the monthly variation of the respiration rate of each bladelet, it is possible to get some suggesting trends. In any of the bases considered, the respiration rate of the 2nd bladelet showed a greater oscillation than those of the other bladelets, with a minimal values in September and two maximal values in November and in February. The high respiration rate on a chlorophyll \( a \) basis in April 1987 of the 2nd bladelet was due to the abnormally low content of chlorophyll \( a \) in the replicate samples used; there is no good explanation for this result.

Seasonal variations of compensation point (\( I_c \)) and saturation onset parameter (\( I_s \))

Both parameters were calculated from the photosynthesis-light curves. As the values were quite similar among the curves irrespective of the different bases, only the values on a frond area basis are used in this paper (Fig. 6).
In the case of \( L \) (Fig. 6A), lower values were found during the spring-summer period, 0.2–0.9 klux (3.3–16.6 \( \mu E \cdot m^{-1} \cdot s^{-1} \)), while higher values were obtained from autumn to the next spring, 0.7–1.7 klux (11.5–31.6 \( \mu E \cdot m^{-1} \cdot s^{-1} \)), with the highest average value in October.

The saturation onset parameter \( I_s \) (Talling, 1957; Kirk, 1983) was higher than 3 klux (60 \( \mu E \cdot m^{-1} \cdot s^{-1} \)). The trend of the seasonal variation of \( L \) was similar to that of \( I_s \), with lower values in spring-summer and higher values in autumn-winter.

**Seasonal variation of chlorophyll content and dry weight**

Figure 7 shows the variations of chlorophyll \( a \) and \( c \) contents per unit area of the bladelet. In all bladelets, the chlorophyll \( a \) content was minimal from November to January, where-from it started to increase (Fig. 7A). The chlorophyll \( a \) content was always lower in the 2nd bladelet and almost always highest in the 11th bladelet. During the winter months all bladelets showed lower values than during spring-early summer period, except for big differences in April 1987.

The chlorophyll \( c \) content was also low during winter time in the new bladelets, which were formed from November to January, but it was high in other seasons (Fig. 7B). Moreover, the pigment content was usually lower in the
younger bladelets (2nd and 5th) than in the older ones (8th and 11th).

In the dry weight per unit area of the bladelet (Fig. 8), there was a clear seasonal variation. A progressive thickening in all bladelets was observed from spring to early autumn, thereafter a quick decrease was measured to reach the minimal values of mid-winter. Usually the oldest bladelets showed higher values than the youngest ones; but in mid-winter the dry weight of the four bladelets considered was quite similar.

**Discussion**

In general, the photosynthetic response of algae can be characterized by the parameters $P_{\text{sat}}$, $I_1$, $I_3$, and dark respiration, allowing easy comparison among the published data (STEEMAN NIELSEN, 1975; DRING, 1982). In this study photosynthesis-light curves were monthly obtained with four different bladelets of *E. cava*. The photosynthetic response of each bladelet was distinct with the position in the blade and with seasons. These results are related to the specific developmental stages monthly encountered on each bladelet. The saturating irradiation recorded in this study is in the range described by LUNING (1981) for mid-sublittoral species, i.e. 150–250 $\mu$E/m$^2$/s$^{-1}$ (7–12 klux). In a recent paper (MAEGAWA et al., 1987), it was reported that the level of light saturation for photosynthesis in young sporophytes of *E. cava* was lower (3–4.8 klux) as a consequence of their understory life and the lower amount of non-photosynthetic tissues (holdfast, stipe and medullary layer); the same trend was found in other Laminariales species (KAIN, 1979; NOVACZEK, 1984). SMITH (1981) also reported much lower $I_1$, (about 2.5 klux) in a brown alga, Lobophora variegata, which forms thick rippled sheets in sublittoral waters, probably due to its higher surface/volume ratio. In several species of Sargassum from the shallow sublittoral zone of the Japan Sea their $I_1$ values were quite similar to those of *E. cava*, while $I_1$ was higher in *S. thunbergii* (MERTENS ex ROTH) O. KUNTZE which inhabits the intertidal zone (GAO and UMEZAKI, 1988) than in *E. cava* of this study.

The shift of low $I_1$ and $P_{\text{sat}}$ values in summer months to high values of winter months in *E. cava* is possibly related to the different thickness of the bladelets as suggested by the results of LUNING and DRING (1985) about light transmittance through algal thallus and also by the results of MAEGAWA et al. (1987) who compared photosynthesis when the blade of young *E. cava* sporophytes was illuminated from one side and from both sides. Thin bladelets and high transparency of seawater reported in this study together with low leaf area index (LAI) (YOKOHAMA et al., 1987) allow high photosynthesis efficiency in mid-winter, but in summer with thick bladelets, low transparency and mutual shading of the canopy (high LAI; see YOKOHAMA et al., 1987) the efficiency of photosynthesis becomes lower. In addition, water temperature is an important factor in the regulation of photosynthetic metabolism by controlling pigment concentration and/or activities of the Calvin cycle enzymes (DAVISON, 1987; DAVISON and DAVISON, 1987). In *E. cava* blade, the slowdown of the growth rate from July, when the seawater temperature goes up higher than 22 °C, was inversely correlated with the reproductive activity (HAROUN et al., 1989). The low $P_{\text{sat}}$ values in June is probably related to an endogenous shift of metabolism from the production of new bladelets to the formation of sori and the reserve of photoassimilates in the summer bladelets.

WHEELER (1980) working with *Macrocytis pyriforma* (L.) C. AG. described that the photosynthesis capacity on a frond area basis of selected fronds increased from the apical to the median blade and then decreased towards the basal sporophylls. ARUGA (1983) recorded the highest $P_{\text{sat}}$ in proximal bladelets of *E. cava* which approximately correspond to the 5th bladelet of this study. MATSUYAMA (1983) obtained the highest $P_{\text{sat}}$ in the longest lobe of Undaria pinnatifida SURINGER f. distans MIYABE et OKAMURA, with a drastic reduction of photosynthesis capacity towards the eroding apical part of the blade.

The seasonal variation of $P_{\text{sat}}$ values is closely related with the physiological stages of the bladelets and the annual growth cycle of the blade (HAROUN et al., 1989). From late spring to early autumn the blade thickened and entered the reproductive period and, at the same time,
P_{\text{max}} decreased in overall bladelets; from November, however, with the onset of new blade formation there was a clear change in the photosynthetic response of the bladelets. In midwinter the bladelets are all fresh and thin, with a high photosynthetic performance. The observed lowering of P_{\text{max}} can be explained by the concurrent thickening of the blade from spring to autumn (Fig. 8), which usually starts from the upper bladelets. In November, the measurements of the 2nd bladelet were carried out on newly developed bladelets with very thin laminae. In general the youngest bladelets showed lower content of chlorophylls compared with the oldest bladelets. Wheeler (1980) with M. pyrifera fronds and Gao and Umezaki (1988) with Sargassum spp. also found less pigments in the youngest parts of the thalli. Another remarkable fact is that the chlorophyll a content of the autumn bladelets, which appeared from November to January, showed minimal values, and from that time on a slow increase was measured for all bladelets (Fig. 7). Thus, the difference in photosynthetic responses can be explained by the rapid increase in dry weight of the bladelets from April to October compared with the slow filling in of chlorophylls. As algae can modify and optimize their photosynthetic systems in an adaptive fashion according to their seasonal light climate (Ramus et al., 1976; Kirk, 1983; Lobban et al., 1985), the blade of E. cava seems to shift its pigment content in relation to the prevailing light conditions.

The big oscillation in the respiration rate of the 2nd bladelet can be explained by the different developmental stages of that bladelet. In September, there was almost no growth in the 2nd bladelet, while in November the autumnal 2nd bladelet was growing very actively, and the new 2nd bladelet of February was also growing very fast. Respiration rates were also greater in the young, upper part leaves of Sargassum spp. compared with the older leaves from lower parts (Gao and Umezaki, 1988).

King and Schramm (1976) described the variation of P_{\text{max}} in two Baltic Sea algae, Fucus vesiculosus and Laminaria digitata, using different thallus portions. In their study, P_{\text{max}} values on a frond area basis were not very distinct among the segments, but on a dry weight basis the subterminal portion showed a higher value compared to the basal portion. In this research we found a positive relationship between the bladelet position and their dry weight per unit area. Following the above-mentioned trend, in E. cava there is a negative relationship between the photosynthesis capacity on a dry weight basis and the bladelet position; the respiration rate was also higher in the youngest bladelet compared with others.

Taking into consideration other studies on E. cava (Ariga, 1981, 1982, 1983; Yokohama et al., 1987) and the previously described annual growth cycle (Haroun et al., 1989) it is possible to define the blade of this species as a "conveyor belt" that would renew its biomass 3 times per year. One blade appears in autumn, with short and thin bladelets having low chlorophyll content. This blade would live until early winter when it is substituted by the winter blade having longer but still thin bladelets with higher content of chlorophylls. Finally, during the summer the blade biomass is composed of long and thick bladelets with a progressive decrease in pigments. In late autumn, large pieces of the blade are broken off and the resultant organic matter will eventually participate in the detrital trophic chains of coastal waters.

The photosynthetic responses of E. cava blade is closely related to its annual growth cycle. The distinct photosynthetic performance of the bladelets is a consequence of their ontogenetic differentiation. Growth and photosynthesis metabolisms seem to be mainly controlled by seawater temperature and light conditions.

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References


鍋田湾における褐藻カジメの光合成特徴の季節変化

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